

# CRYSTAL DEVELOPMENT IN DISCOASTERACEAE AND BRAARUDOSPHAERACEAE (PLANKTONIC ALGAE)

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**ABSTRACT.** In both families the skeleton consists of little rosettes of calcite crystals grouped round a central axis. In the Discoasteraceae the crystals are arranged each with its optic axis parallel with the principal (= central) axis; the individual crystals have a bilateral symmetry with virtual suppression of the trigonal symmetry characteristic of inorganically grown crystals. The Braarudosphaeraceae differ in having their crystals arranged with a cleavage plane at right angles to the principal axis, to which the optic axes are oblique; the calcite is internally laminated parallel to this cleavage, and all three cleavages respond differently to etching. It is suggested that these peculiarities in morphology and chemical behaviour result from biochemical controls exerted by the organism during crystal growth, producing complex internal structures on a very fine scale, yet not fine enough to interfere with the crystal-lattice.

I HAVE commented elsewhere upon the remarkable control which coccolithophorid cells are able to exert over the crystallization of calcite, enabling them to shape the crystals that they secrete with great precision (Black 1963). Two other families of planktonic algae, the Discoasteraceae and Braarudosphaeraceae, share this ability to regulate the growth of crystal faces, and although the resulting patterns are different, the crystallographic control is equally striking.

At present we do not know how this is achieved. The physiological processes leading up to the precipitation of calcium carbonate in the coccolithophorid cell have been investigated in some detail (Paasche 1968, Watabe and Wilbur 1966), and the same general principles are presumably applicable to the discoasters and braarudosphaerids. The morphology of the resulting crystals, on the other hand, is clearly dependent upon controls of a much more specific kind; it is perhaps connected with biochemical peculiarities which are constant in any given species, but vary from one species to another and from one family to another. Looked at in this way, structural details of the crystal-line skeleton may be expected to reflect biochemical characters, at present unknown, but likely to have an important bearing upon the taxonomy of these organisms.

## TERMINOLOGY AND CHOICE OF INDICES

Miller's three-index notation for the trigonal system has considerable advantages over a four-index method for representing the crystal faces in the arms of a discoaster, and for this reason has been adopted here. When the rhombohedron face inclined towards the principal axis is taken as (010), the indices display the bilateral symmetry of a discoaster arm with a clarity that would be impossible if a four-index notation were used.

The word *face* is used in its crystallographical sense, and the obverse and reverse sides of the asterolith are referred to as *surfaces*. Since we do not know which of the two surfaces was external in relation to the cell, we cannot logically speak of them as upper and lower, or distal and proximal. The two surfaces are nevertheless morphologically

unlike, and we can make a crystallographical distinction between the *F surface*, with a ring of rhombohedron faces round the principal axis, and the *E surface* with a little star of radiating polar edges.

### DISCOASTERACEAE

Discoasters are small fossils, commonly between 10  $\mu\text{m}$  and 20  $\mu\text{m}$  in diameter, consisting of calcite crystals grouped radially round a central axis so as to form patterns resembling rosettes or snowflakes (Pl. 89, fig. 4); these structures are commonly referred to as asteroliths. In most species the crystals lie in a single plane, which may be called the principal plane of the asterolith, at right angles to the principal axis, which behaves as an axis of symmetry for the whole body (these are the *Hauptebene* and *Hauptachse* of Stradner, in Stradner and Papp 1961, pp. 48, 49).

*Optical orientation.* One fundamental property of all discoasters is that their constituent crystals are invariably arranged so that the optic axis of each is parallel with the principal axis. In microscope slides prepared in the usual way, with the asteroliths lying flat against the object-glass, they remain dark between crossed nicols, and are thus easily distinguishable from coccoliths and most other nannofossils. Because of this, it has sometimes been assumed that each asterolith consists of a single crystal. This does not, however, necessarily follow from the optical behaviour, since a group of crystals with differently oriented lattices would give the same effect provided that the *c*-axes were all parallel. Examination under the electron-microscope of specimens with recognizable crystal-faces shows that as a general rule each arm of a discoaster is an independent crystal, and it is only in rather special circumstances that several rays are crystallographically united to form a single crystal.

*Crystallographic observations under the electron-microscope.* When discoasters are prepared by standard methods for examination under the microscope, their discoidal shape usually causes them to lie flat upon the supporting film or slide, with the principal plane at right angles to the line of vision. From their optical behaviour in polarized light we know that the trigonal axis of each crystal is then aligned parallel with the line of vision. Hence we can treat electron-micrographs of discoasters as orthographic projections on the principal plane, which coincides with the basal pinacoid {111} of the constituent crystals. This provides a convenient method of working out the development of faces on these crystals, and their relation to the general morphology of the complete discoaster. There is an additional advantage in that the plane of projection {111} is the same as that used in a conventional stereographic projection, and observations made on electron-micrographs can be quite simply related to the positions of poles and the traces of zones plotted on a standard stereogram.

On an orthographic projection, and hence on a suitably oriented electron-micrograph, all edges between faces in the same zone are represented by parallel lines, and the common direction of these lines is normal to the diameter of the zone-circle in the stereogram. By measuring the direction of a crystal-edge on an electron-micrograph we can thus find the projected direction of the zone-axis to which the adjacent faces are related. In the more simply constructed discoasters this is often all that is needed to

confirm the identity of a face recognized by inspection, for experience shows that the faces most commonly developed all have simple indices.

Occasionally the identity of a face can be settled by looking at the symmetry of etch-figures or overgrowths. For example, the basal pinacoid can often be recognized by the presence of overgrowths in the form of regular trigonal pyramids. The orientation of these pyramids fixes the cleavage directions and hence the orientation of the crystal-lattice; it also serves to distinguish (111) from ( $\bar{1}\bar{1}\bar{1}$ ), and thus provides a means of identifying the upper and lower surfaces of an asterolith.

*Simple six-armed discoasters.* These principles can now be applied to some of the very simply constructed discoasters that are found in Tertiary pelagic sediments. Two species of this kind, *Discoaster adamanteus* Bramlette and Wilcoxon, and *D. obtusus* Gartner, can be obtained in an excellent state of preservation from Oligocene and Miocene deep-sea oozes. The shape of the asteroliths is determined entirely by well-developed crystal faces, the actual combination of faces varying slightly in different samples. Specimens of *D. obtusus* resembling the holotype consist of six primitive rhombohedra, and have the simplest structure possible in a six-armed discoaster (text-fig. 1; Pl. 87, figs. 3, 4). In the holotype of *D. adamanteus* the rhombohedra are modified by the addition of faces which give the asterolith a star-shaped instead of a hexagonal outline (text-fig. 2; Pl. 88, figs. 2-4). As seen under a light-microscope, the two holotypes are quite distinct in outward shape, but they are accompanied by a range of intermediate forms in which the extra faces are developed to various degrees. This leads to difficulty in drawing a line between the two species, and raises an interesting taxonomic problem.

The simplest form of *D. obtusus* is hexagonal in outline, and consists of six simple rhombohedral crystals each of which has a polar edge running radially along the middle of the arm, flanked by a pair of steeply sloping rhombohedron faces (text-fig. 1a; Pl. 87, fig. 4). The third rhombohedron face is directed towards the centre, and is much smaller than the other two. Measurements on suitably tilted specimens confirm the identification of the three faces on this surface of the arm as belonging to the primitive rhombohedron  $r = \{100\}$ .

As this unequal development of individual faces belonging to the same form is found repeatedly in the arms of discoasters, it is desirable to adopt a consistent scheme for labelling such faces. For asteroliths constructed on the same plan as *D. obtusus*, with

#### EXPLANATION OF PLATE 87

- Figs. 1-2. *Discoaster adamanteus* Bramlette and Wilcoxon, Middle Miocene, Trinidad (H851). 1, oblique view of *F surface*. Face (010) very small, at the centre; (100) and (001) make the flanks of the arms; (101) is not developed on the *F surface* of this specimen. 24455,  $\times 7500$ . 2, Hemidiscoaster condition, orthographic view of the *F surface*. A simple combination of *r* faces without *e*. Arms 1, 3, and 5 are united to form a single crystal, with suppression of (010). In the alternate arms (010) is represented by very small triangular faces.
- Figs. 3-4. *Discoaster obtusus* Gartner. 3, Hemidiscoaster condition, oblique view of *F surface*. Alternate arms are united to form a single crystal with its trigonal axis at the centre of the asterolith. (100) and (001) are the only faces developed on this surface of the arms. Lower Miocene, Jamaica (H719). 24407,  $\times 12\,500$ . 4, normal (Eudiscoaster) condition, orthographic view of *F surface*. Face (010) is developed as a ring of very small faces surrounding the centre. Compare text-fig. 1a. Lower Miocene, Pacific Ocean (H852). 24420,  $\times 7500$ .





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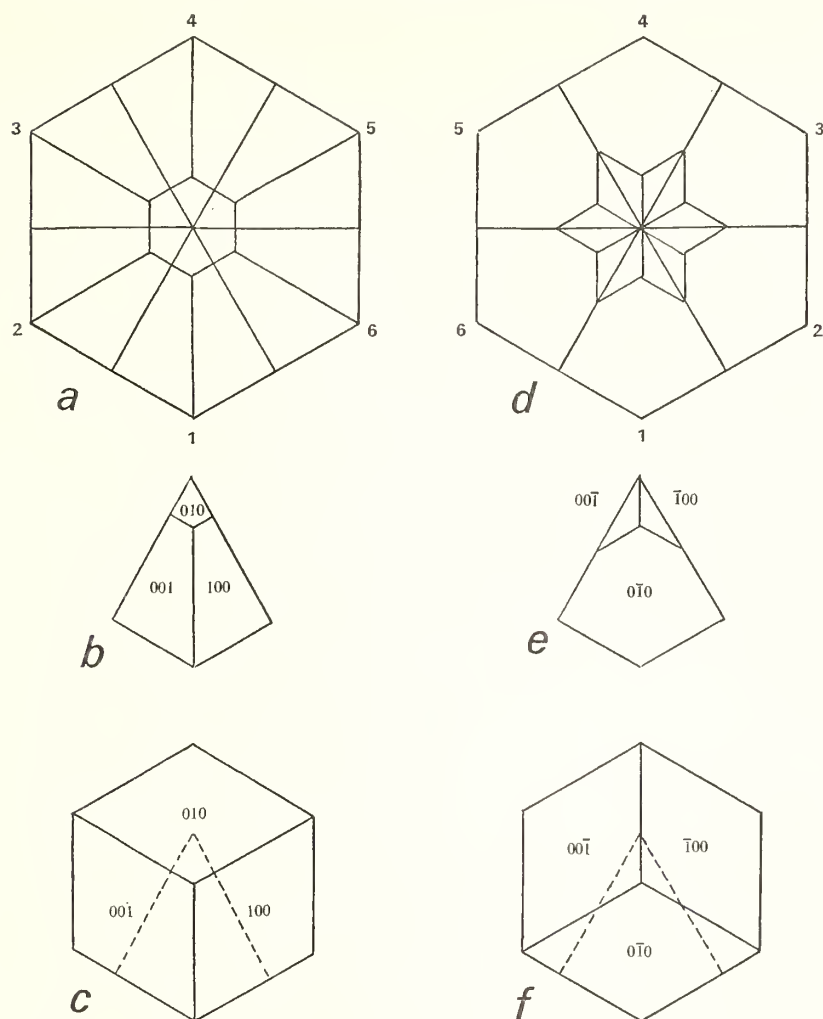
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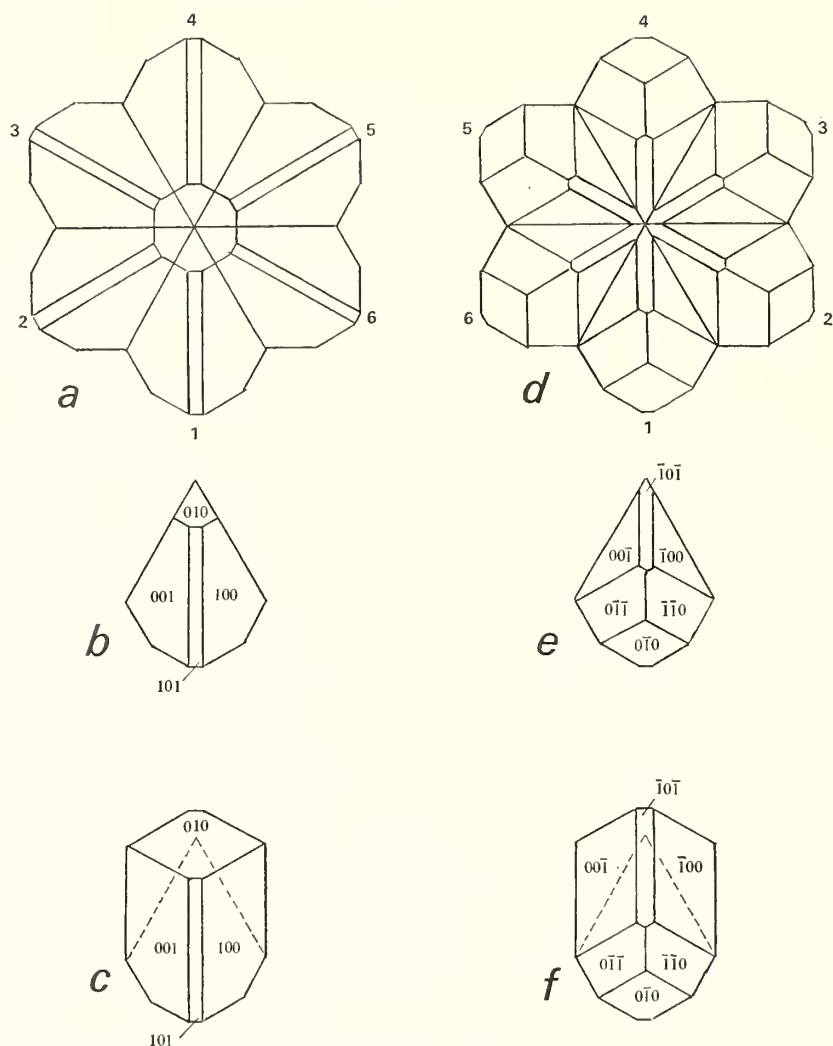
BLACK, Planktonic algae





TEXT-FIG. 1. *Discoaster obtusus* Gartner in orthographic projection on (111). The asterolith consists of six arms, each of which is part of a primitive rhombohedron. *a-c*. *F surface* (face (010) to centre). *d-f*. *E surface* (edge to centre). *a, d*. The complete asterolith; compare Pl. 87, fig. 4 and Pl. 88, fig. 1. *b, e*. A single arm. *c, f*. A single arm in relation to the fully developed rhombohedron.

a crystallographic plane of symmetry running along the length of the arm (text-figs. 1, 2), the *r* face directed towards the centre is selected as (010), and the parallel face which cuts off the tip of the arm on the reverse surface of the asterolith is then (0 $\bar{1}$ 0). The two opposite surfaces of the asterolith can thus be distinguished from each other: one has a ring of crystal faces surrounding the centre, and the other has a set of edges radiating away from it (Pl. 88, figs. 1, 2). They may conveniently be referred to as the *F surface* (face-to-centre, with positive indices for *r*) and the *E surface* (edge-to-centre, with negative indices for *r*). Specimens of *D. obtusus* almost invariably place themselves on



TEXT-FIG. 2. *Discoaster adamanteus* Bramlette and Wilcoxon in orthographic projection on (111). The arms are parts of crystals with a special habit combining the primitive rhombohedron  $r = \{100\}$  and the obtuse rhombohedron  $e = \{101\}$  with unequal development of the faces of both forms.

*a-c. F surface.* *a.* The complete asterolith; compare with Pl. 88, fig. 2. *b.* A single arm. *c.* A single arm in relation to the upper surface of the crystal, in which (101) is developed without (110) and (011). *d-f. E surface.* *d.* The complete asterolith; compare with Pl. 88, fig. 4, which shows a slightly different development of faces. *e.* A single arm. *f.* A single arm in relation to the lower surface of the crystal, which unlike the upper surface includes ( $\bar{1}\bar{1}0$ ) and ( $0\bar{1}\bar{1}$ ).

a microscope slide with *F* uppermost because this side is steeply conical, and the fossils naturally come to rest on the flatter *E surface*.

Each of the six arms shows a similar development of faces successively rotated through an angle of  $60^\circ$ , and since the lattice must also be rotated through the same angle there can be no crystalline continuity between adjacent arms. In the orthographic projection

the solid angles that form the distant ends of the rays give an internal angle of  $120^\circ$ , and six-fold repetition produces a regular hexagon. Electron-micrographs of specimens lying flat on the supporting film show a very close approximation to this ideal shape (Pl. 87, fig. 4).

In examples of *D. adamanteus* agreeing closely with the type (Bramlette and Wilcoxon 1967, pl. 7, fig. 6) the shape of the arms is modified by additional faces belonging to the obtuse rhombohedron  $e = \{110\}$ . The six faces of this form are hardly ever all developed, and the omission of individual faces is always effected in such a way as to emphasize the bilateral symmetry of each arm (Pl. 88, fig. 3; Pl. 89, fig. 2). The crystallographic plane of symmetry running along the length of the arm thus remains operative, whereas the other two planes of symmetry are, in effect, suppressed in the external morphology of the crystal. For example, a pair of  $e$  faces,  $(\bar{1}\bar{1}0)$  and  $(0\bar{1}\bar{1})$ , is conspicuously developed on the *E surface*, whereas the third face  $(\bar{1}0\bar{1})$  is almost invariably suppressed (Pl. 88, fig. 4). These two faces intersect the  $(100)$  and  $(001)$  faces of the *F surface*, producing a notch in the outline of the asterolith at the distant end of each interradiial suture.

In many specimens the obtuse rhombohedron is represented by the  $(\bar{1}\bar{1}0)$  and  $(0\bar{1}\bar{1})$  faces only, and there are no faces belonging to this form on the opposite *F surface*. Occasionally a specimen presenting the *F surface* is seen with each of the polar edges of the primitive rhombohedron  $r$  truncated by a narrow, parallel-sided  $e$  face (Pl. 88, fig. 2); more commonly, however, only  $(101)$  is developed and  $(110)$  and  $(011)$  are suppressed.

A further modification is sometimes introduced by the addition of a basal plane, either  $(111)$  or  $(\bar{1}\bar{1}\bar{1})$  (Pl. 88, fig. 1). The identity of these faces can often be confirmed by the presence of little outgrowths in the shape of equilateral pyramids, which on  $(111)$  have a face and on  $(\bar{1}\bar{1}\bar{1})$  an edge directed towards the centre of the asterolith.

Some of the patterns resulting from these various combinations are shown in Plates 87–89. Judged as discoasters, they all have a primitive appearance. Nevertheless, the organism has clearly exerted a firm control over the growth of its crystals, and in particular has taken considerable liberties with the trigonal symmetry of calcite to achieve some of these results. Each of the six crystals has been prevented from growing larger than a certain pre-determined size, and the pair of faces  $(100)$  and  $(001)$  has been forced to develop quite differently from  $(010)$ . Although the interfacial angles necessarily preserve a trigonal symmetry, the selective development of faces gives an external form suggestive of a much lower degree of symmetry. The triad axis, all three diad axes, and two of the planes of symmetry are suppressed, leaving the third plane as the only operative element of symmetry in the crystal. This imparts a pseudomonoclinic appearance to the outward shape of each arm, mimicking a crystal of the monoclinic clinohedral class. The discoaster gives the impression of obeying the letter of crystallographic law and disregarding its spirit. This becomes more noticeable with increasing complexity of structure; indeed the elaborate shapes achieved by the more advanced discoasters are a measure of their success in overcoming the morphological limitations which trigonal symmetry imposes upon inorganically grown crystals (Pl. 89, fig. 4; Pl. 93, fig. 1).

*Hemidiscoaster structure.* We have already seen that there can be no crystalline continuity between adjacent arms of a six-rayed discoaster, since the crystal lattice is rotated through  $60^\circ$ , giving a different orientation in space. Rotation through  $120^\circ$ , on the other hand, brings the lattices into a parallel position, so that crystalline continuity between



alternate rays is theoretically possible. Fusion of crystals in this way does in fact take place, producing asteroliths in which three of the six rays are united to form a single crystal, separated from the alternate rays by well-marked interradian sutures (Pl. 87, figs. 2, 3; Pl. 89, fig. 2). This structure can easily be seen under a good optical microscope, and was used by Tan Sin Hok (1927, p. 120) to separate the genus *Hemidiscoaster*, with fusion of alternate rays, from *Eudiscoaster* in which all the rays retain their independence. Bramlette and Riedel (1954, p. 394) found it impossible to maintain the distinction between these two genera because several otherwise homogeneous species were found to include both variants. In fact, the special relationship between the crystals in a six-rayed asterolith would lead us to expect such a state of affairs; the possibility of crystalline continuity is always present, but it may well be a matter of chance whether it is actually achieved or not.

*Pauciramous asteroliths.* Some six-armed species of *Discoaster* are accompanied by a few similarly constructed asteroliths which differ in having a smaller number of arms. Some of these have been given separate specific names, but there are good reasons for regarding them as aberrant representatives of the six-armed forms which they otherwise resemble.

Just before its extinction at the end of the Pliocene Period, *D. brouweri* produced an abundance of such pauciramous forms (Pls. 90–92). These clearly are not all of the same kind. In one type, asteroliths with 3, 4, or 5 arms preserve a vestige of hexagonal symmetry in that the angles between the arms are always either 60° or 120°, and under the electron-microscope the stump of an undeveloped arm can often be seen bisecting the wider angle. Pauciramous asteroliths of this kind result simply from the failure of some

#### EXPLANATION OF PLATE 88

Fig. 1. *Discoaster obtusus*, orthographic view of *E* surface. ( $\bar{1}00$ ) and ( $00\bar{1}$ ) make an arrowhead pair of faces pointing towards the centre; ( $0\bar{1}0$ ) is large, sloping outwards. The small equilateral triangles on some of the arms are ( $\bar{1}\bar{1}\bar{1}$ ). In the upper part of the figure, the median edge of the *F* surface is faintly visible through the transparent replica. Compare text-fig. 1d. Lower Miocene, Jamaica (H719). 24413,  $\times 9000$ .

Figs. 2–4. *D. adamanteus*. Lower Miocene, Pacific Ocean (H852). 2, orthographic view of *F* surface. The ring of ( $010$ ) faces makes a small hexagonal crater at the centre; ( $101$ ) is narrow and not developed on all the arms. Compare text-fig. 2a. 22291,  $\times 9000$ . 3, orthographic view of *F* surface with ( $101$ ) in addition to ( $010$ ), ( $100$ ), and ( $001$ ). 22274,  $\times 4500$ . 4, orthographic view of *E* surface. ( $\bar{1}00$ ) and ( $00\bar{1}$ ) are developed as a pair of very small faces pointing to the centre; ( $\bar{1}\bar{1}0$ ) and ( $0\bar{1}\bar{1}$ ) large, ( $\bar{1}0\bar{1}$ ) not developed; ( $0\bar{1}0$ ) is at the outer ends of the arms, not always clearly distinguishable. Compare with text-fig. 2d, which differs in having the additional face ( $\bar{1}0\bar{1}$ ). 24442,  $\times 4500$ .

#### EXPLANATION OF PLATE 89

Fig. 1. *Discoaster* cf. *adamanteus*. *E* surface. Near the centre are ( $\bar{1}00$ ) and ( $00\bar{1}$ ) with the intervening edge truncated by ( $\bar{1}0\bar{1}$ ). The lozenge-shaped face is ( $\bar{1}\bar{1}\bar{1}$ ). ( $\bar{1}\bar{1}0$ ) and ( $0\bar{1}\bar{1}$ ) are relatively large. ( $0\bar{1}0$ ) cuts off the tip of the arm. Lower Oligocene, Pacific Ocean (H861). 24051,  $\times 4500$ .

Figs. 2–3. *D. adamanteus*. Lower Miocene, Pacific Ocean (H852). Hemidiscoaster condition, *F* surface. Arms 2, 4, and 6 fused to form a single crystal, arms 1, 3, and 5 independent. Each arm is a combination of ( $100$ ), ( $001$ ), and ( $101$ ). The asterolith has three radial planes of symmetry. 24435,  $\times 6750$ . 3, *D. adamanteus*, abnormal condition, *F* surface. Arm 2 is fused crystallographically with arm 6, and arm 3 with 5; 1 and 4 are still independent. Each arm is a combination of ( $010$ ), ( $100$ ), ( $001$ ), and ( $101$ ). The asterolith has only two planes of symmetry. 24444,  $\times 4500$ .

Fig. 4. *Discoaster challengeri* Bramlette and Riedel, with bilaterally symmetrical arms giving radial symmetry to the asterolith. Middle Pliocene, Indian Ocean (H845). 24326,  $\times 4500$ .



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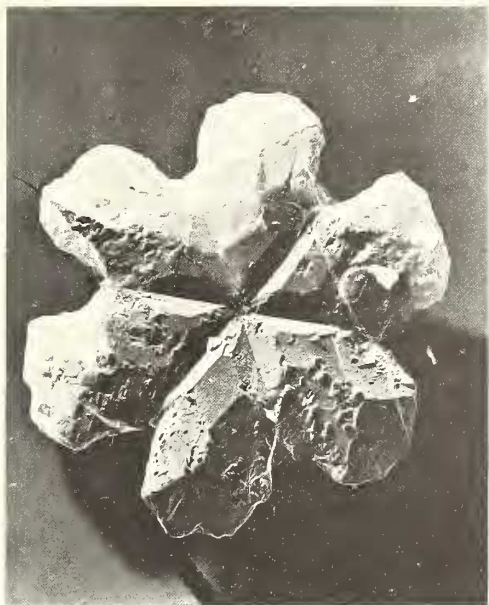
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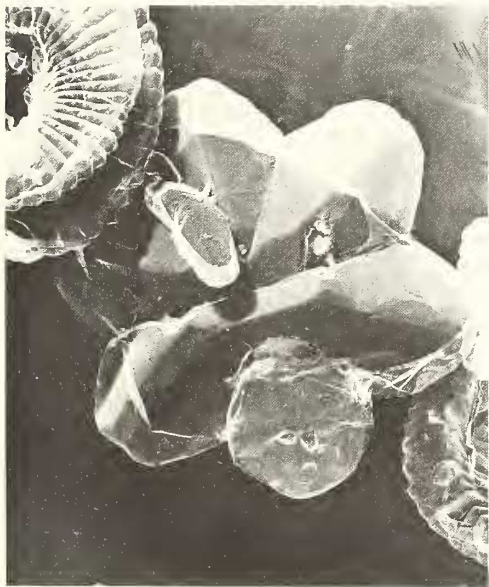




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of the arms to grow to a normal length, and no fresh crystallographic problems are involved (Pl. 90, fig. 3–Pl. 91, fig. 3).

In a second type, there is no vestige of a hexagonal plan, and the asteroliths have a new 3-, 4-, or 5-fold symmetry with angles of  $120^\circ$ ,  $90^\circ$ , or  $72^\circ$  between the arms (Pl. 91, fig. 4–Pl. 92, fig. 3). In asteroliths with four or five arms the general plan of construction is similar to that of six-armed individuals. Each arm is an independent crystal, separated from its neighbours by interrational sutures and presenting a similar face or edge towards the centre. The lattice having been rotated through  $90^\circ$  or  $72^\circ$  in adjacent arms, the crystals are brought into incongruent positions and have sharply defined contacts.

With three-armed asteroliths, the situation is different. By virtue of the trigonal symmetry of calcite, a rotation of  $120^\circ$  brings the lattices of all three arms into the same orientation. The arms then no longer behave as twinned individuals but act as a single crystal with a homogeneous lattice throughout (Pl. 92, figs. 2, 3). For this reason interrational sutures are never found in three-armed discoasters or in *Marthasterites*, which has exactly the same crystallographic structure, and differs only in the sculpturing at the tips of its arms.

*Departures from radial symmetry.* In the great majority of discoasters, the angle between adjacent arms is constant for any particular number of arms, so that the symmetry is truly radial around the principal axis. Occasionally individuals of *D. brouweri* are found to depart from this rule, having the six arms at unequal angles such as  $30^\circ$ ,  $60^\circ$ , and  $90^\circ$ . Such aberrant forms have been observed in other six-armed species, and Gartner (1969, p. 598) has recently described a five-armed derivative of *D. brouweri* as a new species, *D. asymmetricus*, in which unequal spacing is the rule rather than an exception (Pl. 91, fig. 4).

When such forms are examined in detail, it is often observed that the interrational sutures are regularly disposed at angles of  $60^\circ$  or  $72^\circ$ , and that the irregular spacing is caused by a departure from bilateral symmetry in the arms themselves.

Specimens of *D. asymmetricus* from Pliocene oozes in the Pacific Ocean have interrational sutures close to  $60^\circ$ ,  $72^\circ$ , and  $84^\circ$ , which are the sums of possible combinations of  $30^\circ$  and  $42^\circ$ , namely  $30+30$ ,  $30+42$ , and  $42+42$ . The arms themselves are asymmetrical, the length of the arm making angles of  $30^\circ$  and  $42^\circ$  with the interrational sutures. If all the five arms were either right-handed or left-handed, a regular spacing of  $72^\circ$  would result, but if arms of both kinds are combined in a single asterolith the observed angles are inevitably produced.

The six-armed specimen shown in Pl. 92, fig. 4 similarly has interrational sutures making angles of  $15^\circ$  and  $45^\circ$  with the length of the arm, and the introduction of two adjacent left-handed arms gives one angle of  $15+15 = 30^\circ$  and another of  $45+45 = 90^\circ$  instead of the normal  $60^\circ$ .

In asteroliths with this kind of arm, the ideal symmetry about the principal axis is of a rotary nature, and obviously cannot be strictly radial even when the arms are all spaced at equal angles. Further development of this type of construction probably leads to such forms as *D. lodoensis* with falcate arms and a much more pronounced rotary symmetry (Pl. 93, fig. 1). In these more advanced asteroliths recognizable crystal faces are almost invariably replaced by curved surfaces, and the material at present available is not suitable for crystallographic study.